
WHAT SATELLITE IMAGERY AND LARGE-SCALE FIELD STUDIES CAN TELL ABOUT BIODIVERSITY PATTERNS IN AMAZONIAN FORESTS¹

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ABSTRACT

The great problem in biodiversity studies in Amazonia is that the existing data are regionally very biased, whether the question is about species distribution patterns, local species diversity levels, or differences in species diversity and species composition among sites. The surroundings of a few cities and biological stations are relatively well inventoried, while most of Amazonia still remains unknown in these respects. The essential questions are, to what extent can these data be extrapolated, and from where do we most urgently need more data? Quantifying biodiversity is not just a question of how many species there are in one hectare. It is also a question of how many different habitats there are, how much the floras of the different habitats differ from each other, and how many species there are in a given region as a whole. Satellite images are invaluable in studying such regional variability, because they provide an overview of wide areas, even inaccessible ones. The color patterns in satellite imagery enable one to identify and map areas that differ in some way; field studies are then needed to find out whether these differences are significant in ecological and floristic terms. Satellite imagery from Peruvian Amazonia shows variation to such an extent that hundreds of sites need to be studied to document and understand it. Because it would take too much time to identify the thousand or so plant species that can be found in a single hectare of forest, we have developed an inventory method based on indicator species. This makes it possible to monitor large areas relatively rapidly and has revealed some intriguing ecological and biodiversity patterns in Amazonia.

Amazonia comprises a huge block of tropical rainforest, and in spite of the relatively dense network of navigable rivers and the active roadbuilding in some areas, most parts of it are practically inaccessible, at least within the time and budget limits of an average biological field trip. No wonder, therefore, that biological inventories have been heavily concentrated on very few spots, which have then become famous inventory sites that everyone working in Amazonia wishes to visit. In southern Peru we have Cocha Cashu and Tambopata biological stations, with high levels of bird and butterfly species richness. In northern Peru we have the Mishana and Yanamono sites, which had the highest tree species diversity per hectare (Gentry, 1988) until a few years ago, when the 1-ha tree inventory in Cuyabeno (eastern Ecuador) was completed and set the new world record, 307 species (> 10 cm DBH; Valencia et al., 1994). Ecuador also hosts the second 50-ha tree plot in the Neotropics, which is

now being established in the Yasuni National Park and is surpassing diversity estimates (Robin B. Foster, pers. comm.). In Colombian Amazonia there is Araracuara with impressive bird and tree diversities, and in central Brazil there is Manaus, with a high species richness in all groups. These are just a few of the most important sites.

In spite of the dedicated efforts of many field biologists, the total area of forest that has been thoroughly inventoried at these sites is vanishingly small, only a few square kilometers out of the 5 million in Amazonia, and no one knows what there is between these well-visited sites. The situation is like having to map plant diversity of North America on the basis of a few tree inventory plots made, say, in northern California, Yellowstone National Park, and the surroundings of the Niagara Falls, plus some general collections concentrated along the road between New York City and Washington, D.C. So what can we really learn about biodiversity in

¹ This paper is dedicated to the memory of Karl U. Kramer, who described many of the *Lindsaea* species discussed here, and provided valuable help with species identification. I am grateful to numerous persons for collaboration in the field, especially Kalle Ruokolainen, Abel Sarmiento, Richer Ríos, Alberto Torres, Mildred García, Antonio Layche, Melchor Aguilar, Simón Cortegano, Guillermo Criollo, Nestor Jaramillo, Gustavo Torres, César Bardales, Lizardo Fachín, Illich Arista, Isabel Oré, Elina Lusa, and Jaana Vormisto, and to Universidad Nacional de la Amazonia Peruana for logistic support. Jaana Vormisto, Risto Kalliola, and Kalle Ruokolainen gave constructive comments on the manuscript. Financial support for the work has been provided by the Academy of Finland, the STD-3 program of the European Union, and FINNIDA.

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Amazonia on such a basis? Are the established sites truly the hotspots of biodiversity, or is the high number of species found in them only a function of the high amount of collecting effort that has been invested (Nelson et al., 1990)?

In a situation like this, there are many questions one would like to get an answer for. The most fundamental of all is: To what extent can we generalize the results from the sites we know something about? In the case of plant diversity, this translates into finding out whether there are floristically different vegetation types involved, and if so, how these can be characterized and mapped. Quantifying biodiversity in general is not just a question of how many species there are in a hectare. It is also a question of how many different habitats there are, how much the floras of the different habitats differ from each other, and how many species there are in a given region as a whole.

This is where satellite imagery comes into the picture. Since satellite images cover practically the whole earth, they can provide information on even the most remote rainforest areas, and in such a way that an overview of wide areas can be obtained at a glance. The color patterns in the satellite images are created by local differences in how the ground cover reflects sunlight, which depends on many physical properties, such as vegetation structure, color of plant leaves, presence of surface water, presence of bare soil or rock, and many more. Because of this physical basis, it is a relatively safe assumption that whenever there is a color difference between two parts of a single satellite image, there is also some physical difference between the corresponding sites in the field. This is the good news. The bad news is that it is usually impossible to know what these physical differences are unless one has visited the sites in the field. In Amazonia, the only easily recognizable ground cover categories are rivers, cities, roads, and vegetation; also cultivated areas can usually be recognized by their characteristic shape. But to find out more detailed properties of the vegetation (natural or cultivated) at a given site, one needs ground truthing or aerial photographs. Even such a trivial question as whether the vegetation is forest or not cannot be solved on the basis of a satellite image alone; the spatial resolution of the images is not detailed enough to show structural details like trees.

This is why large-scale field studies are needed. Properly processed satellite images soon reveal that even the continuous rainforest is not homogeneous, but rather shows itself as a bewildering mosaic of patches that come in different colors, sizes, and shapes. It is the task of the field studies to find out

how each of the reflectance patterns can be interpreted in ecological and floristic terms. Do the differences in reflectance correspond to floristic differences? Does the degree of reflectance difference reveal the degree of floristic difference? Which are the species that actually occur in each of the recognizable patches? How many different habitats are there in the area as a whole? How many species are there in the area as a whole? How are the different habitats distributed? How restricted are the distributions of the plant species in relation to the habitats?

All these questions can be answered, at least to some degree, if the field studies cover enough area and are carefully planned with the help of the satellite imagery. Field inventories need to include sites in landscape patches with different reflectances to document the differences, but they also need to include some sites in similar patches to document how homogeneous these are. And the inventories need to be rapid; it is not feasible to spend several months at a single site, if there are hundreds of sites to be inventoried. This paper will present results of studies that have been conducted in the northern part of Peruvian Amazonia with these objectives in mind.

BASICS OF SATELLITE IMAGERY

There is an ever-growing body of literature about satellites and satellite images, but much of it is rather technical and therefore alien to the majority of botanists who are not specialized in this particular field. The purpose of this paper is to give the reader an idea of the potential and the problems involved in the use of satellite imagery in vegetation and biodiversity studies by giving a short introduction to those aspects of satellite images that are most relevant in this context. More complete technical accounts can be found in, for example, Harris (1987), Mather (1987), and Lillesand and Kiefer (1994).

The physical basis of satellite images is quite simple: the satellite carries sensors that scan the ground and record the intensity of reflected sunlight. The smallest unit of observation is a pixel, the size of which depends on the kind of satellite and sensor used. In Landsat satellites, which are the most widely used satellites in vegetation studies, each pixel roughly corresponds to a square 80 m by 80 m on the ground when MSS (multispectral scanner) sensors are used, and to 30 m by 30 m when the more advanced TM (thematic mapper) sensors are used. While scanning the terrain, the sensors essentially measure the average reflectance

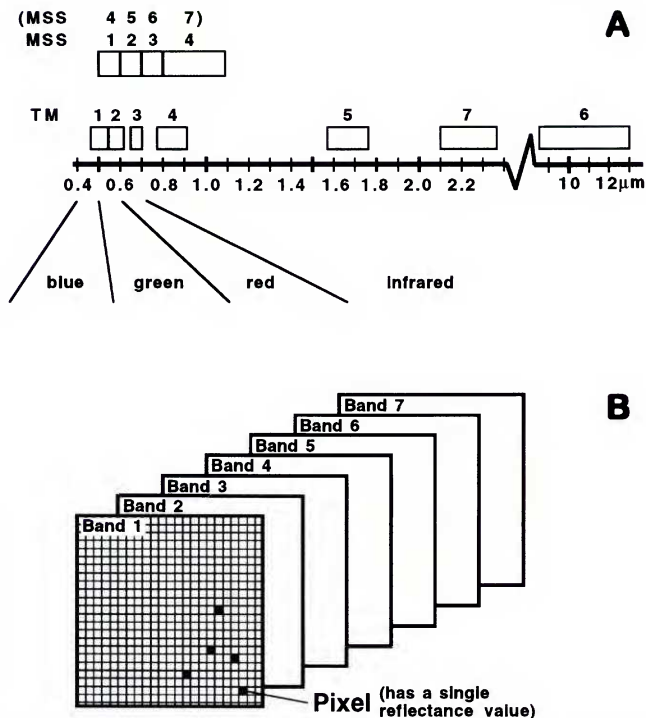


Figure 1. —A. The bands in Landsat MSS and TM data. The numbering of MSS bands has been changed, and therefore older images use a different numbering system (shown in parenthesis) than more recent images. —B. Schematic representation of the data structure in Landsat TM imagery, where each of the seven wavelength bands is recorded in its own data file.

of each pixel on a relative scale and store the measured value into the cell corresponding to that pixel in a spreadsheet database (Fig. 1). In the process, any details smaller than the pixel are lost, and afterward it is impossible to see on the image if a particular pixel contained, say, a house or a group of trees or open field. If such details are needed, they have to be obtained from other sources, like field studies or aerial photographs.

In the satellite, there are several spreadsheets being filled in simultaneously, each by its own sensor that records the reflectance in a certain wavelength band. The MSS is equipped with sensors to

observe four bands, and the TM has sensors for seven bands, including both visible and infrared wavelengths (Fig. 1). Any of the bands in a satellite image can be viewed on a computer screen with the help of an image analysis program. The computer is then told to use the spreadsheet corresponding to the desired band, for example, the one recording green, and to convert the numerical information back to light intensities, in this case to the intensity of illumination of the pixels on a computer screen. The result is a map where those pixels that had a high reflectance for green on the ground are displayed bright on the computer screen, and

those that had low reflectance are displayed dark. At this stage, it is possible to choose any color for the display. The original green can be displayed as green, but it can equally well be displayed as red or blue or (most commonly) gray. It is irrelevant which color is chosen, because the information is here conveyed by the relative brightness of the pixels, not their hue.

Different bands show somewhat different information, because not all surfaces reflect the different wavelengths in a similar way. For example, water tends to absorb infrared, but to have a high reflectance for visible wavelengths, especially blue. Therefore open water areas can appear almost black in images created using the infrared bands, but very bright in images that use the bands of visible wavelengths. Vegetation, on the other hand, has high reflectance for infrared, but very low reflectance for visible wavelengths, especially red and blue, because these are absorbed and used in photosynthesis. Because of these differences, it is usually desirable to view several bands at once to get a better idea of the overall spectral variation in the study area. The easiest way of doing this is to make a color composite using three of the available wavelength bands.

Three bands can be used simultaneously because each pixel on a color computer screen can be thought of as a group of three lamps: red, green, and blue. The hue and brightness of a pixel depend on which of these lamps are lit and how brightly they shine. For example, if only blue is lit, the pixel will appear blue; if red and green shine at equal intensities but blue is not lit at all, the result is yellow, and if the intensity of red is increased relative to the intensity of green, the hue becomes progressively more orange and finally red.

In the process of making a color composite, the computer produces a map with each of the desired bands, assigns each of these to its own color on the screen, and displays the three maps simultaneously on top of each other to produce a full-color image. On displaying a TM image, for example, the reflectance values of band 3 can control the intensities of red on the screen; band 4 can control green, and band 5 can control blue. Obviously there are many other possible combinations that can be used. In fact, because different bands convey different information and hence show partly different patterns in the image, the choice of the band combination is very important. Patterns in an image created with bands 4, 5, and 7 are somewhat different than those in an image created with bands 1, 2, and 3. For vegetation studies, the most useful color composites

are often obtained by combining two near-infrared bands with one visible-light band.

It is important to keep in mind that the actual colors of the final satellite image product have no absolute meaning; they depend on the arbitrary decision on which of the chosen bands was assigned to which of the colors on the computer screen, and as long as the same band combination is used, changing the color assignments makes no difference for the information content of the image although the overall color of the image may change drastically. Of course some color combinations look more pleasing than others and are therefore more commonly used.

In densely vegetated areas with little surface relief, such as lowland Amazonia, most of the surface is green. From an airplane, such areas look rather monotonous with few eye-catching features, and so they look from a satellite, too. This is because there are no big differences in surface reflectance from one site to another, and therefore most of the pixels have reflectance values that are very similar and only represent a narrow range of the possible intensities that the satellite sensor is capable of recording. Consequently, a color composite created with the original satellite data looks relatively homogeneous: there may be a hint of a pattern there, but if the differences in intensity are not big enough, they cannot be confidently recognized or mapped.

Image enhancement is the solution to this problem. There are several ways of enhancing an image, but the main purpose of all of them is to make more efficient use of the different light intensities a computer is able to display. Instead of using just the narrow range of intensities that were recorded in the original spreadsheets of the satellite image, the computer recalculates the reflectance value for each pixel in such a way that the differences are exaggerated and a wider range of possible intensities is used on the computer screen. The process can be compared to adjusting the contrast on a TV screen: if contrast is too low, all patterns on the screen seem fuzzy; if contrast is too high, details are lost; when contrast is optimized, the patterns become clear and easy to recognize.

A more advanced phase in the digital analysis of satellite imagery is the automatic classification of the image to different ground-cover types. There are two principally different methods that can be used to obtain a computer-classified image: supervised and unsupervised classification procedures. In supervised classification, the user selects groups of pixels that represent the different ground-cover types in the area, and the computer then assigns

each of the remaining pixels to one of these classes. In unsupervised classification, the user defines either the number of classes she wants to obtain, or the amount of variation to be allowed within any one class. The computer then creates as many classes as are needed and assigns each pixel to one of these.

Unfortunately, a general drawback of digital classification is the very low reliability of classification within the rainforest realm (see discussion in Tuomisto et al., 1994). Relatively good results can be obtained in areas where there are clear structural differences among the ground-cover types, such as exist among savannas, swamps, and closed-canopy forests. However, distinguishing among different kinds of closed-canopy forest is much more difficult, and hence the degree of error is higher. Another source of error is that, even if the study area is unexplored in the field and it is unknown how many vegetation types there are, the user has to define either the number of classes or the variation allowed within each class prior to analysis. In this way, user-induced bias is easily incorporated into the results, although digital analysis is often advocated as an "objective" method.

A great advantage of unclassified images is that the researcher can be fairly certain that all the patterns that are visible in the product really exist in nature. Fieldwork may later show that not all of them are relevant for the questions at hand, or that some true differences were not recognized, but the risk of creating artificial patterns is small.

Indeed, unclassified but enhanced image products have proved especially useful for the monitoring of large and unexplored rainforest areas, since they are able to reveal spatial patterns whose existence has previously been unknown (Townshend et al., 1987; Kalliola et al., 1991; Tuomisto et al., 1994; Tuomisto et al., 1995). Consequently, such satellite images can be efficiently used in fieldwork planning: they can help in locating sites that represent formerly uninventoried or otherwise interesting vegetation, and they can also indicate to what extent results of fieldwork at any given location can be extrapolated to other locations. For these reasons, the term "satellite imagery" is used in the following text to mean "enhanced, unclassified satellite imagery."

MATERIAL AND METHODS

A preliminary interpretation of satellite imagery was used to identify units that were suspected to harbor different kinds of rainforest vegetation in the northern part of Peruvian Amazonia. An attempt

was then made to select field study sites so that as many of these units as possible were sampled, while attention was also paid to the adequate geographical distribution of the samples. Initially the satellite image interpretation was based on a Landsat MSS scene from 1983 centered around the city of Iquitos (published in Tuomisto et al., 1994), but later a more recent TM scene (from 1993, to be published elsewhere) became available, as well as TM scenes for adjacent areas. The scale of the images used in the visual interpretation was 1:250,000.

The exact locations of the field study sites were chosen with the help of the satellite imagery so as to be both representative of interesting-looking landscape patches (or border zones between patches) and practically accessible by roads or navigable rivers. The primary purpose of the study was to document variation within *tierra firme* (non-inundated) forests, so swamps and seasonally inundated areas were excluded from the sampling whenever they were large enough to be identifiable in the satellite images. However, small swamps in depressions between adjacent hills and floodplains of small creeks occur throughout *tierra firme*, and these were included as a part of the natural variation within the landscape.

The present paper will concentrate on documenting distribution patterns of pteridophytes. In earlier studies (Tuomisto et al., 1995; Ruokolainen et al., 1997) we have found that pteridophytes and the Melastomataceae can be used as indicators of more general floristic patterns, because the floristic similarities among sites as measured with either pteridophytes or the Melastomataceae show a very high correlation with the floristic similarities as measured with trees: the correlation between pteridophytes and trees can exceed 0.8 (Mantel test, $P < 0.001$; Ruokolainen et al., 1997). This is very practical for large-scale vegetation studies, where it is necessary that the sampling at any one site is floristically representative enough to justify regional comparisons. Both pteridophytes and the Melastomataceae are easy to identify and collect compared to trees, because they are smaller in size and include far fewer species. Indeed, the high species diversity of trees makes tree sampling and identification especially laborious, and the number of individuals observed per tree species in any one sample plot is often low (Campbell et al., 1986; Balslev et al., 1987; Gentry, 1988; Valencia et al., 1994; Duivenvoorden & Lips, 1993, 1995; Ruokolainen et al., 1997; see also Clark, 1998, this volume). Consequently, chance can have a great impact on the observed floristic composition, and it is difficult

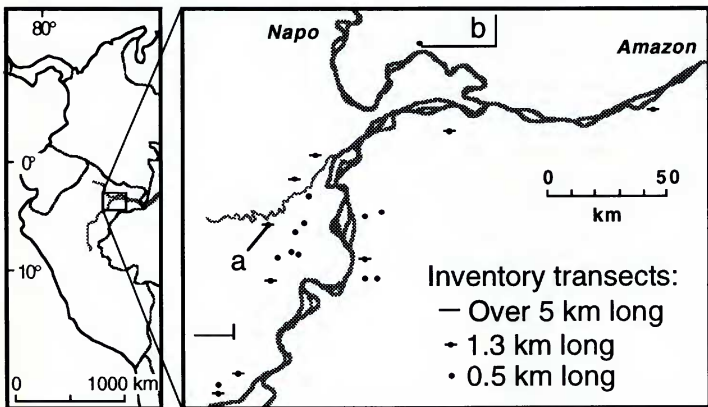


Figure 2. Map of the study area in Peruvian Amazonia with the locations of 23 inventory transects. The transects in Mishana (a) and Sucusari (b) are discussed in detail in the text.

to unravel ecological patterns in the tree species distributions. Focusing the inventories on suitable indicator species makes it possible to sample larger areas and more individuals per species in a shorter time, and consequently it becomes more feasible to work out the possible edaphic preferences of each species. It also becomes possible to evaluate with a higher certainty whether two samples actually belong to the same forest type or not, because each sample contains a higher proportion of the local species pool and the observed similarity patterns are hence more robust.

Because the study was aimed at finding out to what extent edaphic conditions influence the distribution of plant species, sampling was done along continuous, finely subdivided transects. This made it possible to directly compare the changes in floristic composition, species abundance patterns, and environmental variables (such as the nutrient content, texture, and drainage of the soil). Several soil samples were taken from each site for chemical analyses in order to quantify the edaphic differences among and within sites. Details on these analyses will be published elsewhere (Ruokolainen et al., 1997, in prep.).

In all, 23 transects were sampled (Fig. 2), totaling almost 83 km or 22 ha. In most cases, the transects were selected within a uniform area of rainforest as judged from the satellite imagery, but four of the transects were placed so that they crossed

one or several boundaries that were visible in the imagery. These were Mishana (marked with "a" in Fig. 2), Trece de Febrero (15 km S of Mishana), Sucusari (marked with "b" in Fig. 2) and Carbajal (> 20-km transect in the SW corner of the study area).

At each of the fieldwork sites, one of four alternative sampling procedures was followed, depending on the degree of detail required and the time available for studying the site. The field procedures were (1) 500-m-long qualitative transect, (2) 500-m-long quantitative transect, (3) 1300-m-long quantitative transect, and (4) several-km-long semi-quantitative transect. In all procedures, the baseline followed a predetermined compass direction (with allowance made for a 90° angle in four cases). The short transects (less than 2 km long) were 5 m wide, and the longer transects were 2 m wide. In the qualitative transects, a list was obtained of those pteridophyte species that occurred within an estimated 2.5 m on either side of the baseline. The quantitative transects were subdivided into contiguous 5 m by 5 m subunits, and the corners of each subunit were marked; within each subunit, the individuals of each pteridophyte species were counted. The semi-quantitative transects were divided into subunits 100 m long, and for each subunit the presence of pteridophytes within an estimated 2 m on the left side of the baseline was recorded. In the first transect (Mishana, marked with "a" in Fig. 2),

no size limit was applied to the pteridophytes, but in the subsequent transects only pteridophytes with at least one leaf longer than 10 cm were taken into account in order to reduce the time spent on looking for and identifying tiny plantlets. Pteridophytes with leaves less than 5 cm long were excluded from the Mishana data before analysis for the present paper. Epiphytes and climbers were only included if they had green leaves at a height less than 2 m above ground.

Nomenclature of the pteridophyte species is mainly in accordance with the revision of the genus *Lindsaea* (Kramer, 1957) and *Pteridophyta of Peru* (Tryon & Stolze, 1989–1994). However, *Lindsaea lancea* (L.) Bedd. var. *lancea* and *L. lancea* var. *falcata* (Dryand.) Rosenst. are in the present paper treated as good species rather than varieties, because (1) they are easy to recognize in the field at any size > 3 cm, (2) they differ ecologically (*L. falcata* Dryand. grows mainly on decaying wood or litter while *L. lancea* is mainly terrestrial), and (3) they maintain their distinctness even when occurring at the same site and on the same substrate.

RESULTS AND DISCUSSION

DIVERSITY PATTERNS IN PTERIDOPHYTES

The fern genus *Lindsaea* provides an interesting example of diversity patterns at different spatial scales. The 23 transects (Fig. 2) harbored a total of 11 *Lindsaea* species, all of which occurred at more than one site. The number of species at any one site ranged between zero and six, and up to nine species were found in the very long transects (Fig. 3A). Transect length obviously contributed to the high *Lindsaea* species richness of the two longest transects, but among the 0.5–1.3-km-long transects there was no consistent relationship between sample size and number of species found. If only the geographical distribution of the diversity values is observed, it is hard to find any regular pattern in the species richness patterns.

A much clearer picture emerges when the soil characteristics of the sites are also taken into account, because these were clearly related to whether a particular species was present or absent at a given site. One of the species thrives on clay soils that are rich in nutrients (*Lindsaea phassa* K. U. Kramer; Fig. 3B), while two species are restricted to nutrient-poor sandy soils (*L. hemiglossa* K. U. Kramer and *L. tetraptera* K. U. Kramer; Fig. 3K, L). One species can be characterized as a generalist (*L. divaricata* Klotzsch; Fig. 3C), as it can be found almost anywhere save the very poorest and the very richest soils of the region (however, there is some

indication that there are actually two closely related forms with different edaphic preferences involved). All the other species are confined to the relatively poor loamy soils, but even among these species there are some interesting differences in distribution patterns. For example, *Lindsaea bolivarensis* V. Marcano and *L. taeniata* K. U. Kramer are both relatively frequent at some loamy soil sites, but they rarely occur at the same site (Fig. 3H, I).

The general ecological pattern that arises is that there are more *Lindsaea* species adapted to poor soils than to rich soils, and that the genus is also locally most diverse on relatively poor loamy soils. Indeed, the only site with no *Lindsaea* species at all has the richest soils of the 23 sites, and the 3 sites that only had one species each (this species was invariably *L. phassa*) are all among the rich-soil sites. All sites with intermediate to poor soils had more than two species each.

It is important to notice here that terms such as "poor" and "rich" should be understood so that they only refer to the relative soil fertility of the 23 sites reported here, and that they do not imply "poorness" or "richness" in a wider context. The present study was conducted in a limited geographical area, and the sampling is far from complete even for that area. Therefore, it is almost certain that the sites discussed here do not represent the full range of existing soil variation in Western Amazonia, so no matter whether the sites are here called poor or rich, they might all just become "intermediate" if more sites were to be included in the comparison.

In some cases it is obvious that internal heterogeneity within a single transect contributed to the high number of species present. Among the short transects, the most obvious example of this phenomenon is the transect close to the village of Mishana (marked "a" in Fig. 2). This transect crossed the boundary between intermediate loamy-clayey soil to poor sandy soil at about 600 m from the beginning of the transect (Fig. 4; further details on floristic and soil changes at this edaphic boundary have been published in Tuomisto & Ruokolainen, 1994). At that same point, the dominant *Lindsaea* species changed from *L. lancea* (on loamy soil) to *L. divaricata* (on sandy soil). *Lindsaea falcata* was abundant close to the transition zone, with a few individuals at the end of the sandy part. The favored substrate of this species appears to be dead plant material, as it is usually found either on decaying wood or on microsites with thick litter and humus layers. The same is true for *L. guianensis* (Aubl.) Dryand., which is most commonly found on decaying tree trunks. This behavior may explain

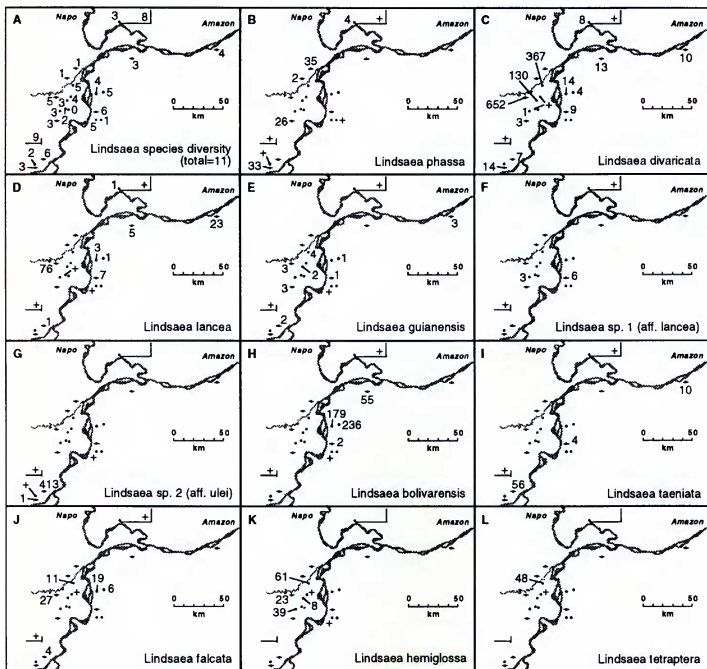


Figure 3. —A. Number of *Lindsaea* species in each of 23 inventory transects. —B–L. Number of individuals of each *Lindsaea* species found in the transects. + indicates that the species was present but the number of individuals was not recorded. The species are shown approximately in the order of decreasing requirements for soil fertility.

why *L. guianensis* is found at sites with widely different soil characteristics and can co-occur with such ecologically different species as *L. phassa* and *L. hemiglossa* (compare Fig. 3E with 3B and 3K). The fifth species found in Mishana was *L. hemiglossa*, which was restricted to the sandy soil at the end of the transect in accordance with its preference for sandy soils at other sites (Figs. 3K, 4).

At a wider scale, spatial variation in species composition can be observed along a 43-km-long transect starting from the river Sucusari (marked "b" in Fig. 2). The most eye-catching feature of the satellite image covering the area is the alteration of lighter and darker patches, which corresponds roughly to the alteration of topographies with lower and higher hills, respectively. The transect har-

bored a total of eight *Lindsaea* species, the distributions of which are shown in Figure 5. As it turned out, transect sections with lower topography tended to have clayey soils, while in the more hilly sections the soils were loamy and poorer in nutrients (the satellite image and the details of the soil analyses will be published elsewhere; Ruokolainen et al., in prep.).

The soil differences were clearly reflected in the species distribution patterns. The distribution of *Lindsaea phassa* was again unlike those of the other species: it was relatively frequent in the beginning and the end of the transect, but entirely lacking in the hilly stretch between km 23 and 38. *Lindsaea taeniata*, *L. lancea*, and *L. divaricata* were also uncommon in this area, but showed otherwise more

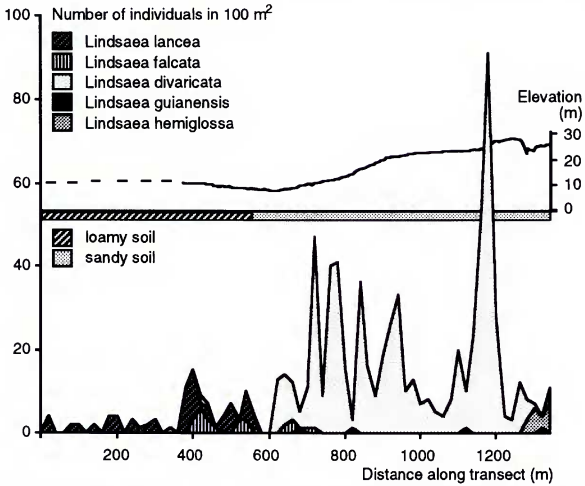


Figure 4. Spatial variation in the abundance of the *Lindsaea* species that were found in the transect in Mishana (for geographic location, see Fig. 2).

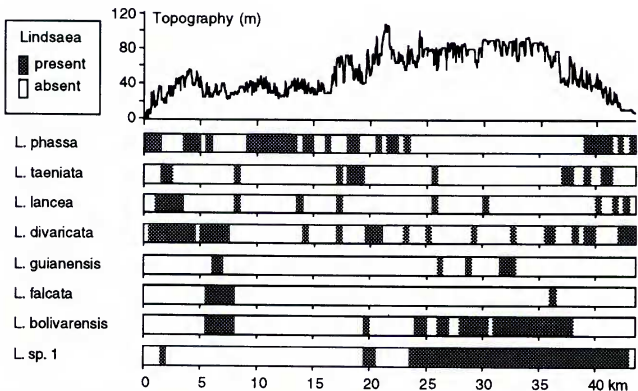


Figure 5. Spatial variation in the occurrence of the *Lindsaea* species that were found in the transect in Sucusari (for geographic location, see Fig. 2).

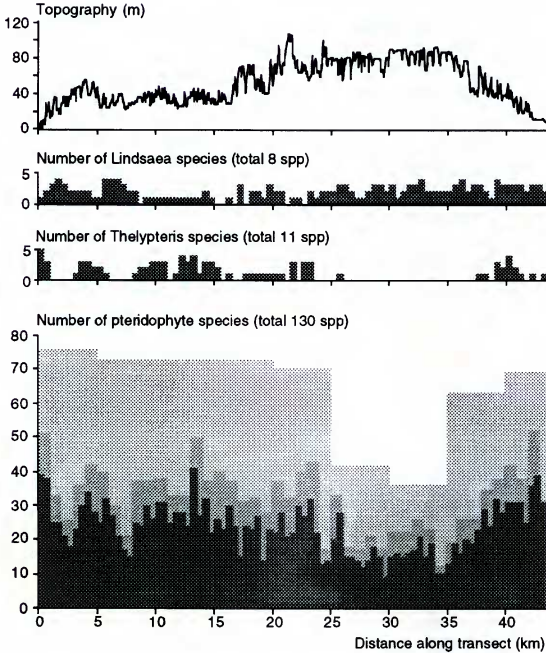


Figure 6. Spatial variation in the species diversity of *Lindsaea*, *Thelypteris*, and pteridophytes in general along the transect in Sucusari (for geographic location, see Fig. 2). For *Lindsaea* and *Thelypteris*, species richness is calculated in sample units 500 m long, and for overall pteridophyte species richness in units 500 m, 1000 m, and 5000 m long.

scattered distributions, and were often present in subunits where *L. phassa* was lacking. The remaining four species were essentially present where *L. phassa* was absent, i.e., in the loamy-soil sections of the transect. *Lindsaea bolivarensis* and an unidentified species of *Lindsaea* were almost confined to the high hills around km 30.

Although the local species richness of the genus *Lindsaea* tends to be higher on poor soils than on rich soils, this is by no means a universal pattern. For example *Thelypteris*, another species-rich fern genus, shows the opposite trend. In the Sucusari transect, *Thelypteris* had no species at all on poor soils, and by far most of the species were found on rich soils (Fig. 6).

The diversity pattern of *Thelypteris* was paralleled by many other fern genera, with the result that

the overall species richness of pteridophytes was clearly higher in rich-soil sections than in poor-soil sections of the Sucusari transect (Fig. 6). This result was found at several different spatial scales. When subunits of 500 m were analyzed, the number of species per subunit ranged between 9 and 41, which is from less than a tenth to almost a third of the total of 130 species in the transect. Obviously the number of species increases with the size of the observed subunits, but even with subunits as long as 5 km, the number of species never exceeded 76 (just over half of the total). In the least species-rich 5-km subunit the number of species was only 36, i.e., less than in the most species-rich 500-m subunits. This shows that diversity patterns depend on local site conditions as much as they do on sampling scales.

The overall tendency for pteridophytes, that species diversity is positively correlated with soil fertility, explains why species diversity and local elevation appear negatively correlated in Figure 6. The geological setting at this particular site is simply such that the poorest soils are found at the highest elevations. Because the Sucusari transect lies entirely within the lowland forest zone (about 100–200 m above sea level), this pattern cannot be explained by the elevation gradient itself: a vertical distance of 120 m is not big enough to cause such elevation-dependent patterns that are found on mountain slopes. The topography is sufficient, however, to expose sediments of different origins and thereby to give rise to significant spatial variation in soils.

ON THE HOMOGENEITY OF THE RAINFOREST

Most *tierra firme* forests are structurally uniform, which is reflected in the paucity of vegetation types recognized for non-inundated areas in Amazonia (e.g., Prance, 1989). Even when this broad category of rainforest is subdivided, attention is usually paid to geomorphology rather than the vegetation itself for the simple reason that geomorphological data are readily available by remote sensing methods, whereas obtaining floristic data requires fieldwork (for examples, see Malleux, 1975; Encarnación, 1985; Duivenvoorden & Lips, 1993; Tuomisto et al., 1994; INRENA, 1995).

When no obvious regional differences have been apparent in *tierra firme*, researchers have tended to assume that these forests are ecologically uniform at broad spatial scales. Therefore, most theories that have attempted to explain the origin and maintenance of Amazonian biodiversity have concentrated on a variety of mainly historical factors. Examples include cyclical changes in climate (Haffer, 1969, 1993; contributions in Prance, 1982; Whitmore & Prance, 1987), intermediate disturbance (Connell, 1978; Salo et al., 1986), random walk (Hubbell & Foster, 1986), and distribution barriers caused by rivers (Hershkovitz, 1968; Salo et al., 1986; Capparella, 1988; Ayres & Clutton-Brock, 1992; Haffer, 1992).

Some researchers have stressed the role of edaphic specialization of plant species in promoting beta-diversity (Gentry, 1981; Young & León, 1989; van der Werff, 1992; Kalliola et al., 1993; Tuomisto & Ruokolainen, 1994; Tuomisto & Poulsen, 1996), but others have argued that the evidence is not yet sufficient to distinguish between random dispersal and edaphic influences (Condit, 1996).

Evidence supporting the ecological differentia-

tion model is accumulating, however. The *Lindsaea* results documented above show that there is systematic floristic variation within the rainforest that can be explained by edaphic specialization of plant species and their differentiated occurrence in different habitats. The pronounced variation in pteridophyte species richness within the Sucusari transect shows also that alpha-diversity can vary considerably among adjacent sites in a predictable manner, even in the absence of physical dispersal barriers. Furthermore, the relationships that were found between local diversity and soils in the plant groups dealt with here (*Lindsaea*, *Thelypteris*, and the pteridoflora in general) seem also to hold for these groups at the continental scale (Tuomisto & Poulsen, 1996). This underlines the difficulty in explaining these patterns by chance alone (cf. Linhart & Grant, 1996).

ESTIMATING SPECIES DIVERSITY

If one wishes to use measured alpha-diversities (species diversity within habitat) to yield estimates of gamma-diversity (species diversity at the regional scale), it is especially important to have a good estimate of beta-diversity (habitat diversity). Reported gamma-diversity (known number of species) in western Amazonia is not strikingly high in relation to the large area involved. The Amazonian lowlands of Ecuador and Peru together cover an area of almost 600,000 km², but only 3100 flowering plants are known from Amazonian Ecuador (Renner et al., 1990) and 7000 from Amazonian Peru (Brako & Zarucchi, 1993). However, the three most species-rich 1-ha tree plots in the world are all situated in this region (Cuyabeno: Valencia et al., 1994; Mishana and Yanamono: Gentry, 1988), and they have about 300 tree species each (> 10 cm DBH).

What is the explanation for this discrepancy between spectacularly high alpha-diversity and much more everyday gamma-diversity? Is the forest so homogeneous that species are hyperdispersed, with beta-diversity being very low, or are so many of the existing habitats unknown that a high proportion of the species have remained undiscovered because their habitats have never been inventoried?

Some species have certainly escaped discovery, which is obvious from the fact that new plant species are continuously being described from Amazonia. In the present study, 2 probably undescribed species were found among the total of 11 *Lindsaea* species, which increases the number of known species by 22%. For several reasons, this may not be a very good estimate of the overall proportion of

undescribed plant species. The fern flora of the Iquitos region is already relatively well collected and known, so in less well-known areas the proportion of undescribed species may be higher. This assumption is supported by the observation that the sites where the two undescribed species were found have not been included in earlier inventories. Furthermore, fern species are generally widespread and relatively well known in comparison with most other plant groups, and therefore the proportion of undescribed species is probably higher among flowering plants than ferns. Finally, different genera must hide different proportions of undescribed species because of differences in their taxonomic complexity and the unequal taxonomic attention that has been paid to them, and we do not know whether *Lindsaea* gives an overestimate or an underestimate of the average among ferns.

What the *Lindsaea* and other fern data (Tuomisto & Poulsen, 1996) do show quite conclusively is that the species are not hyperdispersed; instead, their distributions reflect edaphic conditions. To some degree similar behavior has been shown among trees, but the tree data are less conclusive because tree sample sizes have been too small to represent the local flora well (e.g., Duivenvoorden & Lips, 1993, 1995; Tuomisto et al., 1995; Ruokolainen et al., 1997).

This being the situation, it can be asked how representative the existing herbarium collections are of the overall regional flora. Only a few sites have been studied intensively enough to warrant the claim that their floras are well known, and even though species typical of the vegetation types found at these sites would be well represented in herbaria, species typical of other vegetation types may be entirely absent. Furthermore, many of the existing data come from general collecting trips, which are concentrated along rivers and roads for obvious reasons of accessibility (Renner et al., 1990), so riparian and pioneer species are probably well represented, while species of the forest interior may be much less collected. Other reasons for missing species include preferred sizes of the plants (shrubs are easy to collect whereas lianas are not) and preferred seasons (plants that are not fertile during the collecting trip are ignored). Also, species that have showy flowers and long flowering or fruiting seasons may be collected with a high frequency, while species with infrequent or inconspicuous flowering tend to go unnoticed. All these sources of error need to be controlled if reliable estimates of species numbers are to be obtained.

It is a general problem in large-scale biodiversity studies in Amazonia and elsewhere that the avail-

able herbarium data are not presence-absence data, but rather presence-only data. If a species was found and collected at a given site, it is documented as a herbarium specimen. But if a species was found but not collected at the site, no record of it remains. Therefore it is impossible to distinguish between real absence of a species and apparent absence due to non-collection, which has led to serious biases in defining biodiversity centers in Amazonia (Nelson et al., 1990). This problem can only be solved by systematic sampling efforts that use study plots or other quantifiable methods that provide comparable data for the different sites.

HOW MANY KINDS OF RAINFOREST ARE THERE?

In general, earlier studies have discussed three habitat types within *tierra firme*, differentiated by whether the soil is sand, loam, or clay (Tuomisto et al., 1995; Tuomisto & Poulsen, 1996; Ruokolainen et al., 1997). The same basic division is used in the present paper, with some additional variation being recognized within each of the three main types. The next question is, how well does this represent the variation found in the region? In other words, can we assume "three" to be a reasonable estimate of habitat diversity, or should we expect to find many more habitats if more sites were inventoried? This is a crucial question for biodiversity assessments, but an answer cannot be obtained just by field inventories: the huge amount of work involved especially in tree sampling makes it impossible to establish enough plots to obtain conclusive answers by field surveys alone.

Satellite imagery can efficiently be used to target field inventories, because it reveals both the existing patterns in the landscape, and the easiest ways to access each of the landscape types. Thereby field sampling can be planned so that the amount of effort invested remains reasonable, while the amount of landscape variation that is covered by field inventories is maximized, and unnecessary repetitive sampling within the same landscape type is minimized.

Satellite images give a clear impression of widespread habitat heterogeneity: on the basis of Landsat TM images we have estimated that many more than a hundred biotopes exist in Peruvian Amazonia alone (Tuomisto et al., 1995; see also Kalliola et al., 1991; Räsänen et al., 1993; Tuomisto et al., 1994). The exact number of vegetation types can never be objectively counted (cf. Webb, 1954; Webb et al., 1970; Austin, 1985), but the importance of obtaining some estimate for the number of habitats and the degree of floristic difference among

them can hardly be overestimated in studies that aim at assessing total biodiversity of a given region (see, for example, the discussion in Campbell et al., 1986). The number of habitats can be estimated from satellite imagery, but the degree of difference between them can only be established by field surveys. Both components need to be known in order to estimate how high beta-diversity really is.

Gamma-diversity is essentially the product of alpha-diversity and beta-diversity, so it should be obvious that it cannot be reliably estimated unless both of these components are satisfactorily known. Given the current world-wide interest in biodiversity, it is surprising how little attention the problem of estimating beta-diversity has attracted.

It is noteworthy that, in spite of their clear differences, the 23 fern transects reported in the present paper are according to satellite imagery situated in the most uniform part of Peruvian Amazonia (PAUT, 1993; Räsänen et al., 1993; Tuomisto et al., 1995). The reason that the study was initiated there rather than in one of the more heterogeneous areas is that complete satellite imagery was not available at the time when the work was started, and the northern part of the country was the only area where we knew of any edaphic variation at all in the *tierra firme* forests: we were attracted there by the famous white-sand forests of Iquitos (Gentry, 1981; Encarnación, 1985). Since then, it has gradually become obvious that the white sands form only a very small part of the ecological spectrum in the area, and that most of the variation is actually found within the forests on non-sandy soils.

Within Peruvian Amazonia, Landsat images show both general regional patterns and detailed local patterns, all of which can be postulated to represent ecological and floristic variation in the forest. Obviously only a minute part of the variation has been field verified, but to date we have discovered nothing that would contradict this interpretation. It is interesting to note that changes between the biotopes may take place gradually over long distances or more abruptly, and regional variation is found in the relative abundances of the different kinds of ecotones (Tuomisto et al., 1995). In some inundated areas the vegetation patches are elongated in shape and have a uniform general orientation, in others they are narrow and aligned according to the river courses. In *tierra firme* areas, large smooth-edged patches are typical in northern Peru, while smaller and more abrupt patches are frequent in the central to southern parts of the country (Tuomisto et al., 1995). Such differences in landscape structure may have important implications for the biota (Dunning et al., 1992; Taylor et

al., 1993), but they have not been paid attention to in either the planning or the interpreting of ecological, floristic, and biodiversity studies in Amazonia.

GEOECOLOGICAL CONSIDERATIONS

Western Amazonia has been the scene of a wide variety of geological events during different eras, which has resulted in considerable heterogeneity of terrain at different hierarchical levels (Salo & Räsänen, 1989; PAUT, 1993; Räsänen et al., 1993). For example, large parts of Peruvian Amazonia have been influenced by sea incursions and fluvial dynamics since the late Cretaceous, and therefore the region consists of a mosaic of edaphically and geomorphologically different areas (Salo et al., 1986; Hoorn, 1993; Räsänen et al., 1987, 1992, 1995). Soil characteristics such as nutrient content, texture, and water permeability are determined, among other things, by the geological formations from which the soils are derived, and by the length of time they have been subject to weathering.

Because of the apparent edaphic specificity of many plant species and habitat types, geological formations with special geochemical characteristics and different ages are especially interesting from ecological and biogeographical points of view. Examples include the Pastaza fan with its Holocene (younger than 10,000 years) volcanoclastic material (Räsänen et al., 1990, 1992) and the Pebas formation with its marine or brackish sediments from the Miocene (Hoorn, 1993; Räsänen et al., 1995). Both of these formations can give rise to soils that are chemically unlike anything else in Amazonia and can therefore be expected to harbor edaphically specialized plant endemics.

It is noteworthy in this context that the Pastaza fan area has been designated an uninteresting area for biodiversity conservation by a workgroup that selected priority areas on the basis of known endemism and diversity centers (Workshop 90, 1991). Very few biological specimens have been collected in the Pastaza swamplands, which has resulted in a low number of known species. However, the geological characteristics of the area suggest that it is ecologically unique and should be prioritized in conservation planning (Kalliola et al., 1996). At the very least, the area should be given special attention when biological collection trips are planned in the future.

CONCLUSIONS

Satellite imagery can be efficiently used in rain-forest studies to recognize different habitats and to map their extent even in areas that are difficult to

get to in the field. This provides an unparalleled tool for studies whose aim is to reach regional conclusions on species diversity. For this purpose, all the habitats that are recognized in satellite imagery have to be field-documented in order to verify to what degree they are floristically distinct, and to quantify species diversity within each of them. Neither local nor regional species diversity can be read directly from satellite imagery, but once the species composition of each of the different habitats has been clarified, diversity estimates for unvisited areas can be obtained by using satellite imagery to correlate them with one of the already field-documented habitat types.

Indicator species can be used with great success to facilitate recognizing floristically different habitats. Thereby they can also be used to predict distribution and diversity patterns of other plants and animals, but only when it has been clarified by field surveys how these relate to the defined habitats. It is not possible to predict the diversity of such organisms for which this background information is lacking, because different plant and animal groups can show opposing diversity patterns.

Only about a dozen vegetation types are usually recognized in Amazonia, and consequently ecological research results are often generalized as representative of "the tropical rainforest." Satellite image analyses show that the extent of heterogeneity in Peruvian Amazonia is such that extrapolations of field results are not warranted without more detailed vegetation mapping, and there obviously is a great need for well-planned work in this field. It is almost ironic that the digital phase in satellite image analysis can be reduced to running a spectral enhancement and printing a hardcopy of the result, which can be accomplished by an experienced analyst in a few hours. Thereafter, it can easily take an experienced botanist a lifetime to finish the fieldwork needed in order to find out what the different color patterns really mean in terms of the diversity of habitats and species.

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